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Phylogenetic Implications of Shell Microstructure in the Pseudomonotidae, Extinct Bivalvia

NORMAN D. NEWELL¹ AND DONALD W. BOYD²

ABSTRACT

A *Pseudomonotis* species (superfamily Aviculopectinacea) from glaciomarine Permian rocks of Western Australia shows remarkable features in wall microstructure different from those of other pseudomonotids. Electron micrographs show well-preserved microstructures similar to those of gryphaeid oysters while most other morphological characters of this and other pseudomonotids ally them with the Aviculopectinidae.

X-ray diffraction analyses show that the entire shell of these fossils consists of calcite rather than aragonite, unlike other pseudomonotids. The good preservation of biogenic structures in the calcite indicates that the mineral is original, not an alteration from aragonite, and is possibly an evolutionary effect of secretion in a cold-water environment.

INTRODUCTION

Among the few available taxonomic characters of fossil bivalve molluscs, the microstructure and mineralogy of the shell are generally regarded as taxonomically useful. However, much work remains to be done. We know that there was a homeoplastic change toward the end of the Paleozoic in several lineages from regular crossed-lamel-

lar aragonite to irregular foliate calcite shells. But the time and manner in which the changes occurred are not yet determined.

Our search for exceptionally well-preserved specimens of Upper Paleozoic bivalves has been fruitful (Newell and Boyd, 1970, 1975, 1985). With such rare material, and aided by the scanning electron micro-

¹ Curator Emeritus, Department of Invertebrates, American Museum of Natural History.

² Research Associate, Department of Invertebrates, American Museum of Natural History; Professor of Geology, University of Wyoming, Laramie 82071.

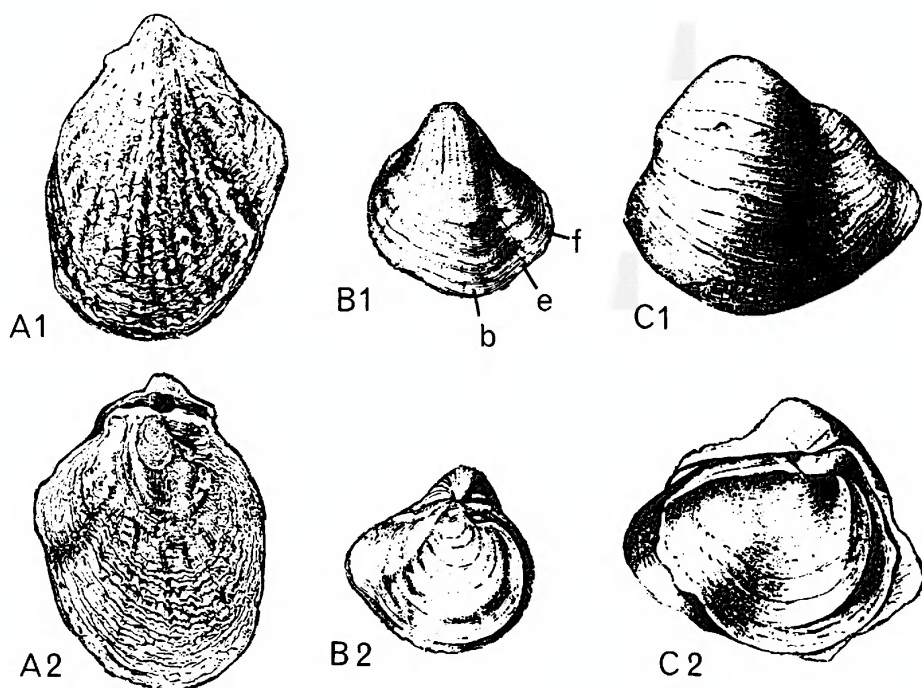


Fig. 1. Comparison of pseudomonotids and a gryphaeid oyster. A1. Left valve of *Pseudomonotis (Trematiconcha) wandageensis*, L. Perm., Australia; A2. Attached right valve of same; B1. Left valve of *Pseudomonotis speluncaria*, U. Perm., England. e indicates the exhalant sulcus; b marks the location of the palliobranchial fusion point on the interior of the shell; f is the posterior flange; B2. Attached right valve of same; C1. Attached left valve of *Gryphaea convexa*, U. Cret., New Jersey; C2. Free right valve of same. (Figures after Newell and Boyd, 1970)

scope (Boyd and Newell, 1984), we have discovered significant details not previously known.

While working on a monograph of oyster-like Permian bivalves (Newell and Boyd, 1970), we encountered an extraordinarily well-preserved *Pseudomonotis* in collections at the University of Western Australia, in Perth, from the Lower Permian (Artinskian) Wandagee Formation (Hocking et al., 1987). The specimens had been collected and freed from matrix, but not described, by Curt Teichert when he was a staff member of that institution. Based on these specimens, we named a new species and subgenus *Pseudomonotis (Trematiconcha) wandageensis* (fig. 1A).

Pseudomonotis is not an oyster. It is an aberrant scallop, an aviculopectinacean with an oysterlike habit of fixation.

The first undoubted oysters are represented by the Gryphaeinae (fig. 1C), a subfamily that was widely distributed when it first appeared

in the Upper Triassic. They are separated by many millions of years from the Paleozoic pseudomonotids. Nakazawa and Newell (1968) described a *Lopha*-like bivalve from the Upper Permian of Japan (fig. 2). If correctly identified this would be a member of the Ostreinae and the oldest known true oyster. However, it is not similar to the pseudomonotids.

At the present time the oysters represent one of the most specialized and successful of all molluscan groups and few marine animals have been more intensively studied. In spite of this, their ancestry has long been in doubt and we agree with Stenzel (1971) that they probably are diphyletic.

The evident phylogenetic importance of the Australian *Pseudomonotis* so excited our interest that Newell, accompanied by his wife, Gillian, and Richard Grant, of the Smithsonian Institution, returned to Teichert's original locality and obtained the instructive specimens described herein.

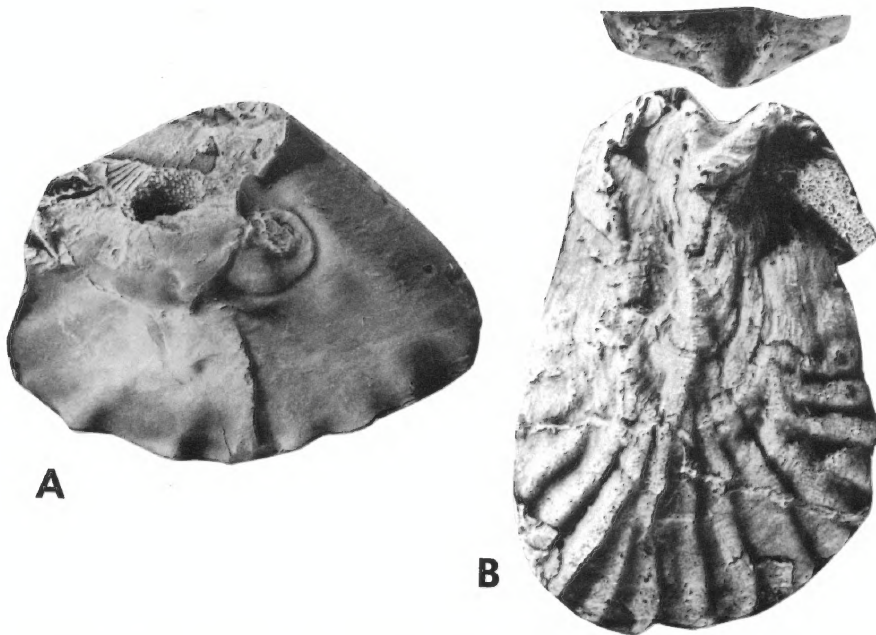


Fig. 2. *Lopha? murakamii* Nakazawa and Newell (1968), $\times 3$. Gujo Formation, Upper Permian, Japan. A. Natural mold of interior of left valve showing adductor scar; B. Latex cast of exterior of attached (left?) valve (dorsal view above). University of Kyoto.

To our surprise, the scanning electron microscope, not available to us in our 1970 study, revealed wall characteristics unlike those of other Aviculopectinacea—relatively thick foliate calcite layers similar to the gryphaeid oysters. We regard this new evidence as support for our hypothesis that the Upper Paleozoic Pseudomonotidae were probably progenitors of the gryphaeid oysters (Newell, 1960; Newell and Boyd, 1970). The replacement of the pseudomonotids as a group by the oysters may qualify as a macroevolutionary event.

THE PROBLEM OF OYSTER ANCESTRY

The oysterlike form, habit, and structural details of the pseudomonotids (fig. 1A, B) are all suggestive of close relationship to the more specialized oysters. Stenzel (1971: 1056–1062, 1224) gave cautious approval of our hypothesis of pseudomonotid ancestry for the gryphaeid oysters (Newell and Boyd, 1970). But T. R. Waller (1978) and C. M. Yonge (1978), leading students of the bivalves, were more impressed by differences than similarities. They emphasized loss of the foot in the oys-

ters (a derived character), versus its retention in the pseudomonotids, and the difference in attachment orientation in the two groups, dextrality in pseudomonotids and sinistrality (also a derived character) in oysters. These experts did not visualize resupination by a simple mutation in early development. They favored a more primitive, but unspecified, dimyarian ancestor while they regarded the many similarities as convergent adaptations to a similar mode of life.

There are, indeed, a few striking morphological differences between pseudomonotids and oysters. Judging from a byssal notch in the right valve, pseudomonotids retained the foot (probably as a gill-cleansing organ) after cementation (fig. 1A-2, 1B-2).

Conversely, larval oysters lose the foot and byssus at the time of cementation and lack a byssal notch. Oysters always become attached by the opposite (left) side, a circumstance so unusual in the subclass Pteriomorpha that we consider the oysters as secondarily resupinate.

It is interesting that the shells of both oysters and post-Paleozoic scallops are predominantly foliaceous calcite while most pseudomonotids and other Paleozoic aviculopec-

tinaceans (exception the Australian examples cited herein) made their shells mainly of crossed-lamellar aragonite (Newell, 1937; Newell and Boyd, 1970).

Following the prodissoconch stage the oyster adds shell increments of calcite, unlike most Pteriina which secrete both aragonite and calcite at the growing margin of the inner and outer layers. In both groups the choice of the mineral used seems to be genetically controlled.

In both groups the outer layer of the right valve, at least in juveniles, consists of simple calcite prisms. The outer layer in left valves varies. In some cases it is lost in oysters. In adult aviculopectinaceans it may be prismatic, fibrous, foliate, homogeneous, or even lacking.

Locomotion in oysters is not possible after cementation. The velum, byssal gland, and foot are lost, leaving relict anterior pedal muscles of unknown function (Stenzel, 1971). Since there is no foot, there is no foot aperture for the byssus. These are all derived specializations that disqualify the *Ostreina* as a stem radicle.

The ligaments in both oysters and most Paleozoic scallops are alivincular with an external, more or less central resilium lodged in a triangular depression and bordered in front and behind by flat interareas known as "bourelets" (Newell and Boyd, 1987).

There is another primitive commonality that joins the oysters and most Pectinina. In many, perhaps most, genera of the two suborders the inner, rigid part of the shell does not reach the free margin. The overlapping outer prismatic layer of the right valve, especially in juveniles, is flexible (Newell and Merchant, 1939; Dickins, 1963; Waller, 1972; Stenzel, 1971). This flexible fringe bends against the inner face of the more convex left valve, providing a tight seal when the shell closes.

The location of an exhalant pseudosiphon is indicated on the exterior of gryphaeid and pseudomonotid shells by a posterior sulcus (fig. 1) above the palliobranchial fusion point, the branchitellum (Newell and Boyd, 1970: 232).

These several traits are characteristic not only of many adult pseudomonotids and aviculopectinaceans but also of gryphaeids.

Together with the new evidence of a gryphaeid-like wall structure in the Australian species, these facts support our view that the pseudomonotids are morphologically intermediate, or transitional, between aviculopectinids and oysters. There are no more probable candidates known to us for the immediate ancestry of the oysters.

SHELL MINERALOGY

Aragonite and calcite are mineral polymorphs of calcium carbonate which, in a matrix of impervious conchiolin, compose the bivalve shell. The organic matrix protects the hard part of the skeleton in living bivalves from great fluctuations of pH. Aragonite is metastable and more soluble than calcite under ordinary conditions of fossilization. In older fossils it is commonly either leached away or converted to recrystallized calcite in which the biogenic microstructure is obscured or lost (e.g., Carter and Tevesz, 1978).

The prodissoconchs of living bivalves are composed of aragonite which was also the component of the inner part, the endostracum, of the mature shell in most Paleozoic Pteriomorphia. The discovery by Runnegar (1984, 1985) of phosphatic replicas of what appears to have been nacre in Cambrian bivalves reinforces the consensus view that this aragonitic microstructure preceded others. Late in the history of some lineages (e.g., Pectinacea, Ostreacea), calcite became dominant with the near elimination of aragonite (Carter, 1980) except for the thin middle layer, the hypostracum. Waller (1978: 345) remarked that his suborders *Ostreina* and Pectinina developed calcitic microstructures from simple prismatic structure by mid-Paleozoic time. This may be a mistake; we know of no such examples.

SIGNIFICANCE OF SHELL MICROSTRUCTURE

O. B. Bøggild's (1930) seminal work on microscopic fabrics of Recent and fossil molluscan shells demonstrated the taxonomic value of the overall microstructure; however, its evolutionary or environmental significance remains obscure. As we show here, not all taxa display stable patterns of microstructure. In any case, the appropriate emphasis

to be placed on given microstructures should be worked out separately for different taxa.

Of the four major microstructures in bivalves, two or more may occur in individual shells. These are: prismatic, nacreous (always aragonite), crossed lamellar (usually aragonite), and irregular foliate and fibrous (calcite). Prismatic structure occurs in both calcite and aragonite. Much later work, by many investigators, has resulted in recognition of several varieties among the main types of bivalve microstructure, as summarized by Carter and Clark (1985).

MICROSTRUCTURE AND MINERALOGY IN PSEUDOMONOTIDAE

Our previous studies of Carboniferous and Permian pseudomonotids indicated that both valves consist of three unequal layers. The inner and middle (hypostracum) layers, originally aragonite, are usually altered to calcite, as in other Aviculopectinacea (Newell, 1937). In those forms a thin outer layer of short calcite prisms covers the right valve and a "homogeneous" or foliated calcite film covers the left valve.

Where the aragonite inner layer in aviculopectinaceans has altered to recrystallized calcite, its original composition may be inferred from its contrast with the outer, less modified calcite layer which frequently retains much of the original biogenic structure.

Selective leaching of the inner aragonite layer is indicated in shells that exhibit fine details of the outer surface but lack internal features such as muscle scars and hinge. The inner layer is missing in many of our silicified specimens of American Permian pseudomonotids, having been leached away before the outer layer was silicified (e.g., Newell and Boyd, 1970: fig. 23E).

SPECIAL ASPECTS OF THE AUSTRALIAN MATERIAL

The topographic morphology of our Australian material is that of typical *Pseudomonotis* but the shell is thin for its relatively large dimensions (around 2 mm in a specimen 75 mm high), and the microstructure and mineralogy are different from those of other species of the genus.

The inner layer is discontinuous, consisting of "linear" (sensu Carter and Clark, 1985), crossed-foliate calcite with first-order folia, 12–18 μm thick, perpendicular to shell surfaces (figs. 3C, 4B). The outer part consists of two intergrading structures. The thicker of these has irregular complex folia of calcite (figs. 3A, B; 4) at low angles to, or parallel with, shell surfaces. This structure is similar to that of oysters and continues into the hyote scales (fig. 7A).

The scales of the left valve are relatively large and modified at their distal margins where the folia are replaced by loosely packed, irregular, simple calcite prisms perpendicular to the surface (fig. 6). The prismatic structure continues as a film over much of the upper valve (fig. 7B). In the lower (right) valve the prismatic structure seems to be limited to marginal wedges (fig. 7A) and a patch of the beak.

The preservation of an inner layer with distinct microstructure is very rare in aviculopectinaceans, and we had at first assumed that this part of the Australian shells must be original aragonite. To our surprise, repeated x-ray diffraction analyses by the American Museum's Department of Mineral Sciences, and the University of Wyoming's Department of Geology, showed only calcite.

This poses an intriguing question: did original aragonite of the middle (hypostracum) and inner (endostracum) layers convert to calcite without blurring the biogenic structure, a result for which we know no precedent, or was the crossed-foliate structure of the inner layer secreted as calcite, a phenomenon unknown until now among Paleozoic pteriomorphians? An argument in favor of the improbable first alternative (conversion of aragonite to calcite during fossilization without loss of biogenic details) is difficult to support. The alternative possibility, that the calcite is primary, is supported by the fact that the foliated structure of the Australian shells resembles that of the calcite of gryphaeids and most modern scallops (Carter and Clark, 1985: 60), unlike that of aragonitic bivalves. The inclination of crossed laths is irregular in calcite shells and usually flatter than in aragonite.

Limited variation in wall "stratigraphy" and mineralogical details among species of a

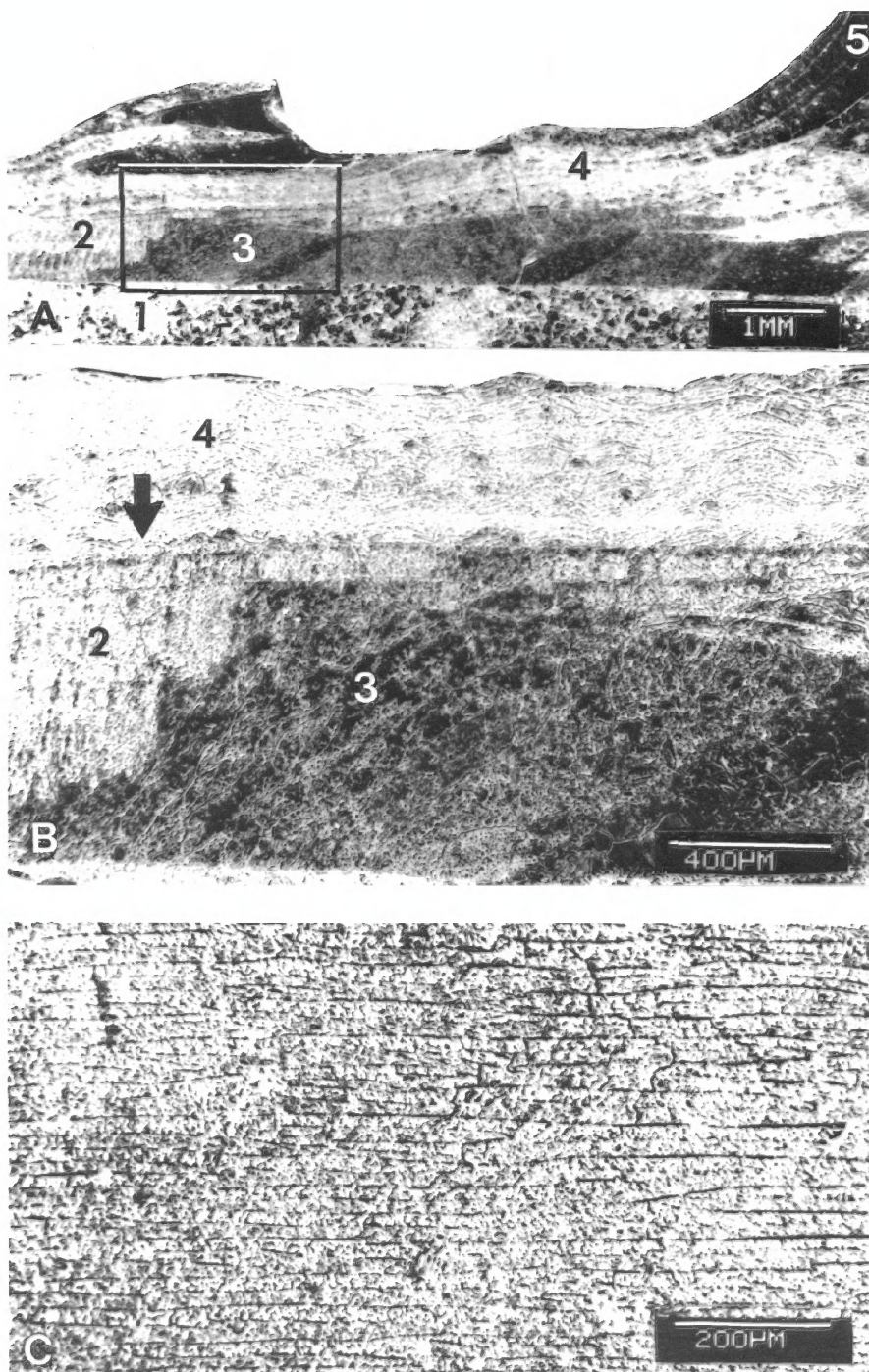


Fig. 3. *P. (Trematiconcha) wandageensis*. SEM photographs, etched sections of left valve. Topotype AMNH 43277. Approximate location a in figure 5. A. Transverse vertical section cut parallel to hinge, $\times 12$. In upward sequence: 1. rock matrix; 2. "linear" crossed-foliate calcite layer in irregular columns; 3. coarsely recrystallized equivalent of 2; 4. irregular foliate layer including thin hyote scales; 5. irregular prisms of thick marginal hyote scale; B. Detail of same outlined in A, $\times 50$; C. Crossed-foliate calcite layer 2 of both A and B; horizontal surface at level marked in B by arrow, $\times 100$.

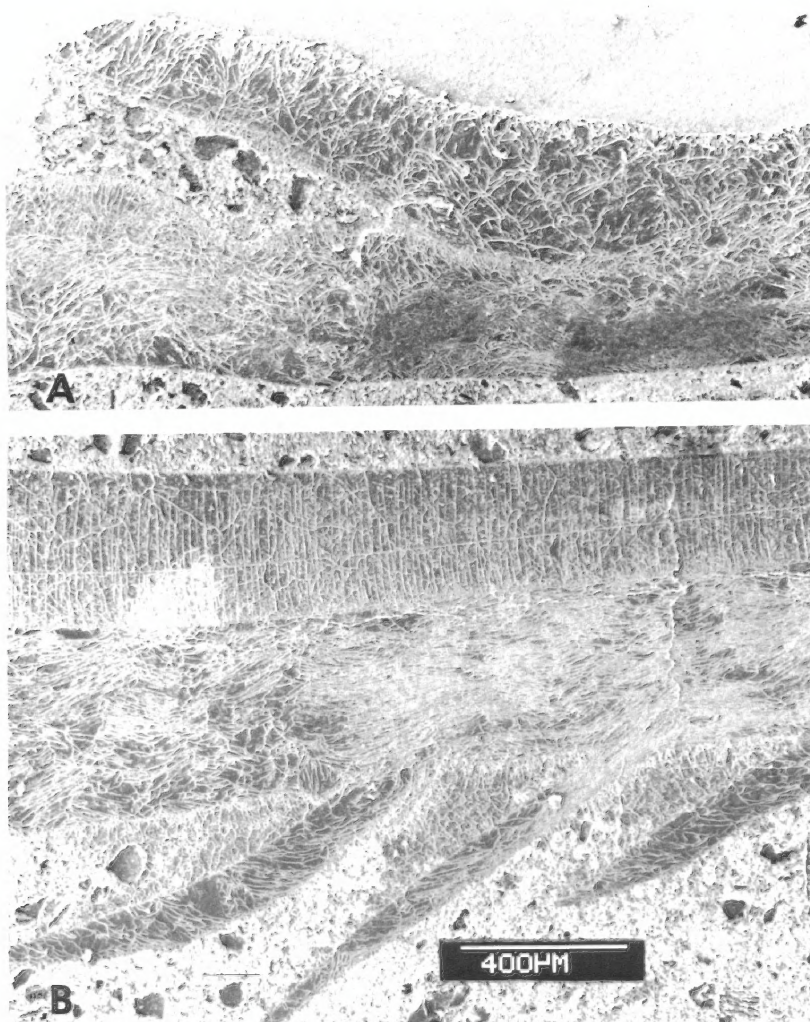


Fig. 4. Median radial sections (beaks at right) of a single articulated specimen of *P. wandageensis*; topotype AMNH 43276. Approximate locations **a** and **b** in figure 5. SEM photographs ($\times 50$) of cellulose peels of etched surface. The thin white lines are spaces originally occupied by conchiolin matrix. **A**. Left valve cut through a hyote scale (inner surface below); main part of shell is irregular foliate with a thin film of irregular prisms above (see also figs. 6B and 7B); **B**. Right valve. Inner surface and crossed-foliate layer above; below, irregular foliate calcite and hyote scales lacking prismatic layer.

few modern bivalves is correlated with differences in habitat temperature. Lowenstam (1954: 307–308) noted that living *Mytilus californianus* from cold waters has an outer layer of calcite prisms whereas warm-water *M. perna* of the Philippines has an outer layer of aragonite nacre. He also cited a difference between the outer layer of warm-water and cold-water species of *Chama* (Lowenstam, 1963: 155). In the former the outer layer is constructed of crossed-lamellar aragonite,

whereas in the latter it is built of calcite with inclined prismatic structure.

According to J. G. Carter (letter of June 16, 1988) “in the Bivalvia, temperature effects on mineralogy appear to be limited to changes in the proportion of aragonitic and calcitic shell layers which are present in both warm and cold water individuals (e.g., *Mytilus californianus*), and to the abundance of calcitic mineralogical aberrations within a predominantly aragonitic outer shell layer

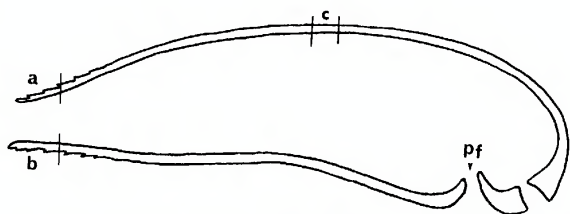


Fig. 5. Diagrammatic median radial section indicating location of sections of figures 3, 4, 6, and 7. *pf* is the pedal foramen, the special character of subgenus *Trematiconcha*.

(rarely observed, primarily in the Veneracea). There is no evidence from Lowenstam's (1954) data, or any subsequent data, that modern or fossil bivalves have changed the mineralogy of an entire shell inner layer from aragonite to calcite as a result of, or even in

correlation with, low environmental temperature."

Diverse calcareous and aragonitic shells occur in many unrelated taxa that live side by side through a wide range of temperatures and pH. With this caveat in mind we note that our Australian pseudomonotid was collected in periglacial strata associated with granite dropstones (Dickins, 1978). Probably the water temperature was low as compared with the temperature around reef-tract Texas *Pseudomonotis* in which the inner layer certainly was composed of aragonite (Newell and Boyd, 1970).

There is a suggestion that this may be a general phenomenon among Gondwanaland aviculopectinaceans. Observations on Western Australian *Deltopecten* by Dickins (1957) and our own examples of *Deltopecten* and

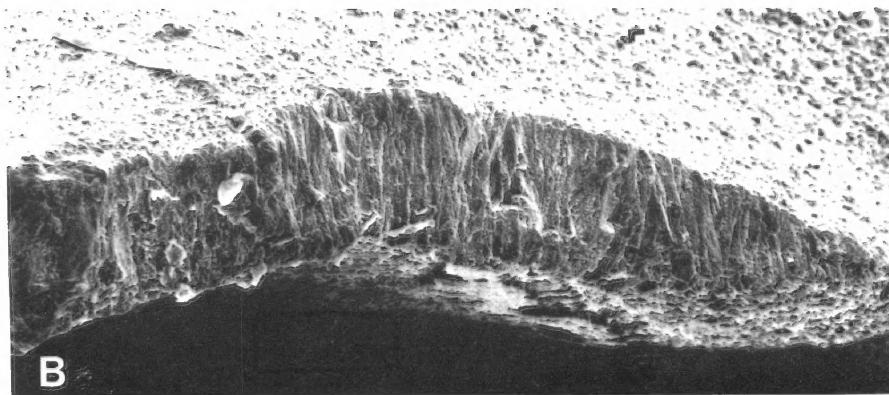
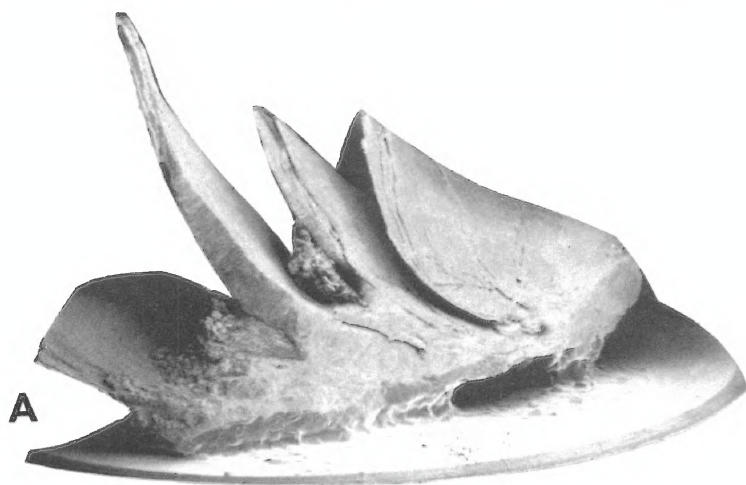


Fig. 6. *P. (Trematiconcha) wandageensis*. SEM photographs, left valve, hyote scales composed of irregular prisms of calcite, at location *a* of figure 5. Topotype AMNH 43277. A. $\times 10$; B. Same, $\times 50$.

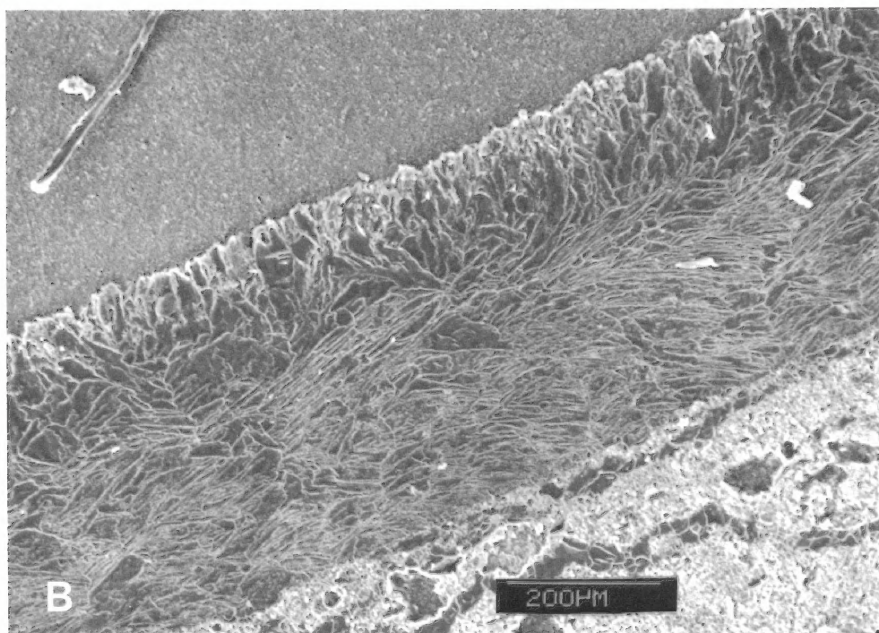
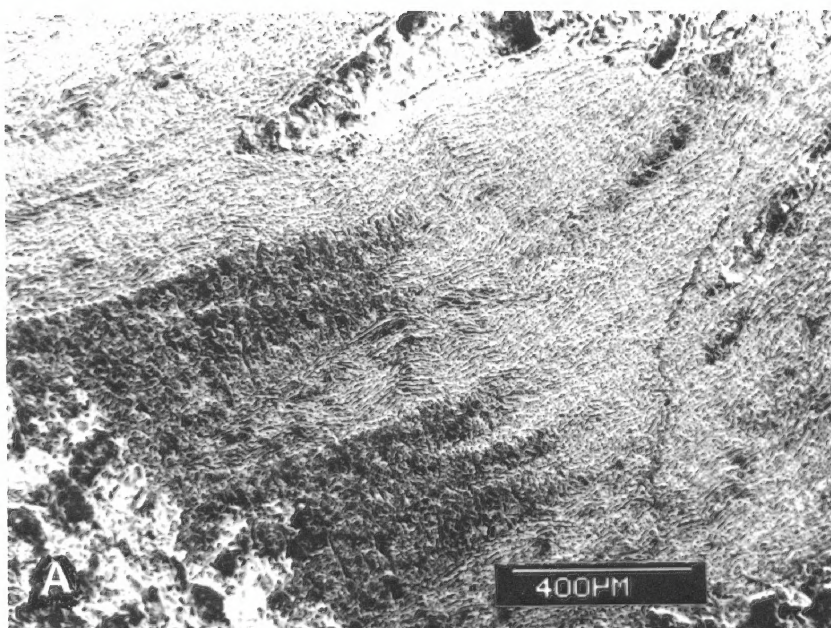


Fig. 7. *P. (Trematiconcha) wandageensis*. SEM photographs. Topotype AMNH 43276. **A.** Right valve, posteroventral fringe margin. Etched surface showing irregular prismatic wedges in irregular foliate calcite at location **b** in figure 5; **B.** Left valve, median radial section, $\times 50$; etched cellulose peel at location **c** of figure 5. Top area shows featureless cellulose peel; middle section has two layers: irregular prisms above, irregular folia below; bottom of photograph is rock matrix.

Etheripecten from the Lyons and Byro groups of the same region are composed of well-preserved irregular calcite folia parallel to, or inclined at, low angles with the shell surface.

CLASSIFICATION

Fossils serve as direct, although incomplete, evidence for a history of life and they

provide tests of phylogenies inferred from living organisms. Fossils tell of the former existence and distribution of past organisms in time and place, such as the pseudomonotids, that would otherwise be unknown. Almost all fossils belong to extinct species, so comparisons with living organisms must be group categories that do not permit the tracing of detailed lineages. Therefore, inferences about relationships generally must be based on the circumstantial evidence of phenetic resemblances and stratigraphic position (Patterson, 1981). But another kind of resemblance can arise from evolutionary convergence (Newell and Boyd, 1978). The question with the Pseudomonotidae is how to assess the historical significance of their morphological characters.

The geologically oldest known member of the family Pseudomonotidae thus far recognized is the rare Lower Carboniferous

Pachypteria (Newell and Boyd, 1970). Pseudomonotids are only slightly more abundant and diverse in the Upper Carboniferous (Newell, 1937). The known record finally reaches an acme in marine Permian rocks of the Northern Hemisphere (Newell and Boyd, 1970). Representatives of pseudomonotids are frequently cited as occurring during the Triassic and Jurassic, but we place them in other families (e.g., Monotidae, Oxytomidae).

The precise taxonomic placement of the pseudomonotids within the subclass Pteriomorpha continues to be controversial. Our preference, with slight modification, is the arrangement in the Treatise on Invertebrate Paleontology (Newell, 1969) in which shell form, general morphology, and geologic age of the available fossils are combined with comparative anatomy and habits of similar living forms.

Omitting taxa not pertinent to the present discussion, the hierarchy that we favor is as follows:

- Subclass Pteriomorpha (Ord.-Rec.)
 - Order Pterioda (Ord.-Rec.)
 - Suborder Pteriina (Ord.-Rec.)
 - Superfamily Pteriacea (Ord.-Rec.)
 - Superfamily Aviculopectinacea (Ord.-Jur.)
 - Family Pterinopectinidae (Ord.-Jur.)
 - Family Aviculopectinidae (L. Carb.-U. Jur.)
 - Family Buchiidae (U. Carb.-Cret.)
 - Family Pseudomonotidae (L. Carb.-U. Perm.)
 - Superfamily Pectinacea (L. Carb.-Rec.)
 - Suborder Ostreina (Perm.-Rec.)
 - Superfamily Ostreacea (U. Perm.-Rec.)
 - Family Gryphaeidae (U. Trias.-Rec.)
 - Family Ostreidae (U. Perm.-Rec.)

The following alternative has been suggested by Waller (1978):

- Superorder Pteriomorpha (Ord.-Rec.)
 - Order Pterioda (Ord.-Rec.)
 - Suborder Pteriina (Ord.-Rec.)
 - Order Ostreoida (Ord.-Rec.)
 - Suborder Ostreina (Perm.-Rec.)
 - Superfamily Ostreacea (Perm.-Rec.)
 - Suborder Pectinina (Ord.-Rec.)
 - Superfamily Aviculopectinacea (Ord.-Jur.)
 - Superfamily Buchiacea (incl. Pseudomonotidae, Monotidae) (L. Carb.-Jur.)
 - Superfamily Pectinacea (L. Carb.-Rec.)

Introduction of Ostreoida to cover both oysters and scallops strikes us as undesirable since most scallops are not oysterlike, nor were they derived from any oysterlike stem group. The true oysters (*Ostreina*, *Ostreacea*) are a specialized group which did not arise until late in the history of the Pteriomorphia.

Both Yonge (1978) and Waller (1978) favor some unknown nonpleurothetic, equi-valve, dimyarian form for the progenitors of the oysters. They emphasize differences whereas we emphasize similarities. We are more impressed by mutual resemblances among larval oysters, pearl clams, and aviculopectinids, which unite them in a single order, the Pterioidea.

CONCLUSIONS

This study supports our theory that the gryphaeid oysters, a major Mesozoic-Cenozoic group, descended with modification from the extinct Permian pseudomonotids, a branch of the aviculopectinacean scallops. The evidence is based on phenetic similarities among shared primitive characters and stratigraphic succession.

The oysters represent a major split from the Pseudomonotidae in the acquisition of a few novel specializations, among which are the foliaceous calcite shell, sinistral attachment, and loss of the foot.

An irreversible change from aragonite to calcite in Permian Gondwana aviculopectinaceans may be a reflection of adaptation to life in cold waters.

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The SEM photographs were taken at the American Museum by Andrew Simon and Newell. Professor Joseph Carter, University of North Carolina, helped with the identifi-

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